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Trophic ecology of *Gymnodactylus geckoides* Spix, 1825 (Squamata, Phyllodactylidae) from Caatinga, Northeastern Brazil

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Abstract

The diet of lizards is mainly composed of arthropods. It can be affected by biotic and abiotic factors, which influence the energy supply provided by the composition of the animal´s diet. The richness and abundance of many arthropod species can be influenced by environmental seasonality, especially in the Caatinga ecoregion, due to the rainfall regimes. The present study aims to describe aspects of the seasonal and morphological variation in the lizard *Gymnodactylus geckoides* diet and their energy content. We collected 157 individuals (63 females, 68 males, and 26 juveniles) at the Catimbau National Park, Northeastern Brazil, of which 72 were analyzed for the dry season and 59 for the rainy season. Our data indicates Isoptera to be the most common prey in *G. geckoides's* diet. Energy content, prey number was higher in the dry season, whereas prey volume and glycogen content increased in the rainy season. Proteins and lipids did not show marked differences. The present study represents the first effort to understand variations in *G. geckoide*'s trophic ecology, indicating that this specie presents a wide variation in their diet, especially when considering seasonal factors, revealing their needs and restrictions according to prey availability and environmental conditions.

Kurzfassung

Die Nahrungszusammensetzung von Eidechsen kann von biotischen und abiotischen Faktoren beinflusst werden und besteht großteils aus Arthropoden. Die Vielfalt und Häufigkeit vieler Arthropodenarten kann durch Umweltsaisonalität beinflusst werden, insbesondere in Caatinga aufgrund der Niederschlagsverteilung. Die vorliegende Studie zielt darauf ab, Aspekte saisonaler und morphologischer Variationen in der Ernährung der Eidechse *Gymnodactylus geckoides* sowie ihren energetischen Inhalt zu beschreiben, wobei 157 Individuen (63 Weibchen, 68 Männchen und 26 Jungtiere) im Catimbau-Nationalpark im Nordosten Brasiliens gesammelt wurden, 72 davon in der Trockenzeit und 59 Tiere in der Regenzeit. Unsere Daten zeigen keinen sexuellen Dimorphismus bei *G. geckoides*, wobei Isoptera die Nahrung dominierten. Unter Berücksichtigung der Ernährung und des Energiegehalts unterschieden sich Beutezahl, Volumen und Glykogenmenge zwischen den Jahreszeiten und zeigten während der Trocken- und Regenzeit jeweils höhere Werte, während Proteine und Lipide keine Unterschiede zeigten. Die vorliegende Studie stellt den ersten Versuch dar, Variationen der trophischen Ökologie von *G. geckoides* zu verstehen, unter Berücksichtigung des Einflusses von Saisonalität, Geschlecht und Morphologie sowie des energetischen Inhalts der aufgenommenen Beute. Sie weist auch auf ein hohe Variation in der Ernährung der untersuchten Art hin, insbesondere im Bezug auf saisonale Umgebungen, was ihre Bedürfnisse und Einschränkungen je nach Beuteverfügbarkeit und Umweltbedingungen aufzeigt.

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Key Words

biochemistry, gecko, prey composition, prey selection

Schlüsselwörter

Beutezusammensetzung, Beuteauswahl, Biochemie, Gecko

Introduction

Ecological studies on diets of lizards have contributed significantly to the development of several theories, including community succession, evolutionary processes, behavioral patterns (Huey et al. 1983; Caughley 1985; Vitt and Pianka 1994), foraging and life history traits (Colli et al. 2003; Recoder et al. 2012), and comparative biology (Costa et al. 2008). Lizards display ecological variations influenced by seasons (Ferreira et al. 2017; Mamou et al. 2019), as well as variations in morphology and behavior (Bock and von Wahlert 1965; Losos 1990), especially neotropical lizards, revealing real challenges in establishing a general life history model (Colli et al. 2003).

Studies on energy support and trophic ecology are crucial for understanding evolutionary biology, natural history (Colli et al. 2003), and energy allocation (Franzini et al. 2019). Moreover, the search for adequate nutrition presents a challenge for many lizard species, influencing their physical conditions (Cooper and Vitt 2002; Mamou et al. 2019). This search can be influenced by biotic factors, including morphometric differences between females and males (Bolnick et al. 2002; Bolnick et al. 2003), and abiotic factors, including environmental changes (especially seasonal environments) and food availability (Díaz and Carrascal 1993; Martins et al. 2008; Ferreira et al. 2017). For neotropical lizards inhabiting the Caatinga biome (Vitt 1986; Jorge et al. 2020), food availability seems to be highly associated with unpredictable seasonality and precipitation levels (Nobre et al. 2008; Vasconcellos et al. 2010a, b; Ferreira et al. 2013).

Studies concerning energy balance and stomach content, reveal available biochemical components (proteins, lipids, and glycogen) and are crucial for understanding evolutionary history traits and how ecological aspects could lead to dietary differences (Cooper and Vitt 2002; Pafilis et al. 2007). Most lizard species are predators of small animals, including arthropods. However, there is a lack of published information concerning the dietary habits of neotropical lizards, especially with regard to the biochemical components of their diet.

Gymnodactylus geckoides is endemic to the Caatinga (Alcântara et al. 2019), and several studies have reported its dietary composition (Vitt 1995; Souza-Oliveira et al. 2017; Alcântara et al. 2019), a possible difference in diet between the sexes (Vitt 1986; Souza-Oliveira et al. 2017) and its relationship with their morphology (Vitt 1995; Souza-Oliveira et al. 2017). Although there are recent data on the diet of *G. geckoides* and its morphology, information from Caatinga remains restricted to the populations from the Exú municipality, Pernambuco (Vitt 1986; Vitt 1995) and Aiuaba and Barro municipalities, Ceará (Alcântara et al. 2019). Moreover, studies reporting energy values of ingested prey or seasonal variations in the diet of the species could provide helpful information about their energy needs and use of the available food resources in the environment; however, these remain scarce.

Recent studies have demonstrated adaptations in lizard feeding due to environmental seasonality and landscape changes, leading to variations in the number and volume of ingested prey (Ferreira et al. 2017; Franzini et al. 2019; Mamou et al. 2019). Thus, the *G. geckoides* diet varies seasonally and between sexes, depending on morphology and prey type, number, volume, and energy values. Therefore, the present study aimed to describe and update the information on the trophic ecology of *G. geckoides*, considering a population from a Caatinga remnant in Pernambuco state, Northeast Brazil. We verified variations in the prey type, number, volume, and energy values of stomach contents, emphasizing seasonal, morphological, and sex variations.

Materials and methods

Study site

This study was performed in Catimbau National Park (8°24'00"S to 8°36'35"S and 37°09'30"W to 37°14'40"W), a protected area (PA) created by a federal decree in 2002. The area features conformations of the Caatinga biome, located at the center of Pernambuco, in the Ipanema Valley, and encompasses the municipalities of Buíque, Ibimirim, and Tupanatinga (Proença 2010) (Fig. 1). The PA area is approximately 62,300 ha and covers altitudes between 500 m to 1,000 m above sea level (ICMBio 2019). The climate is semiarid and strongly seasonal, with an annual precipitation between 0 and 256 mm and the highest rainfall levels between March and July (ICMBio 2019; INMET 2019). The landscape includes evergreen and deciduous forest, with shrubby spineless vegetation, sandy soils, and rock fields (Sousa et al. 2012).

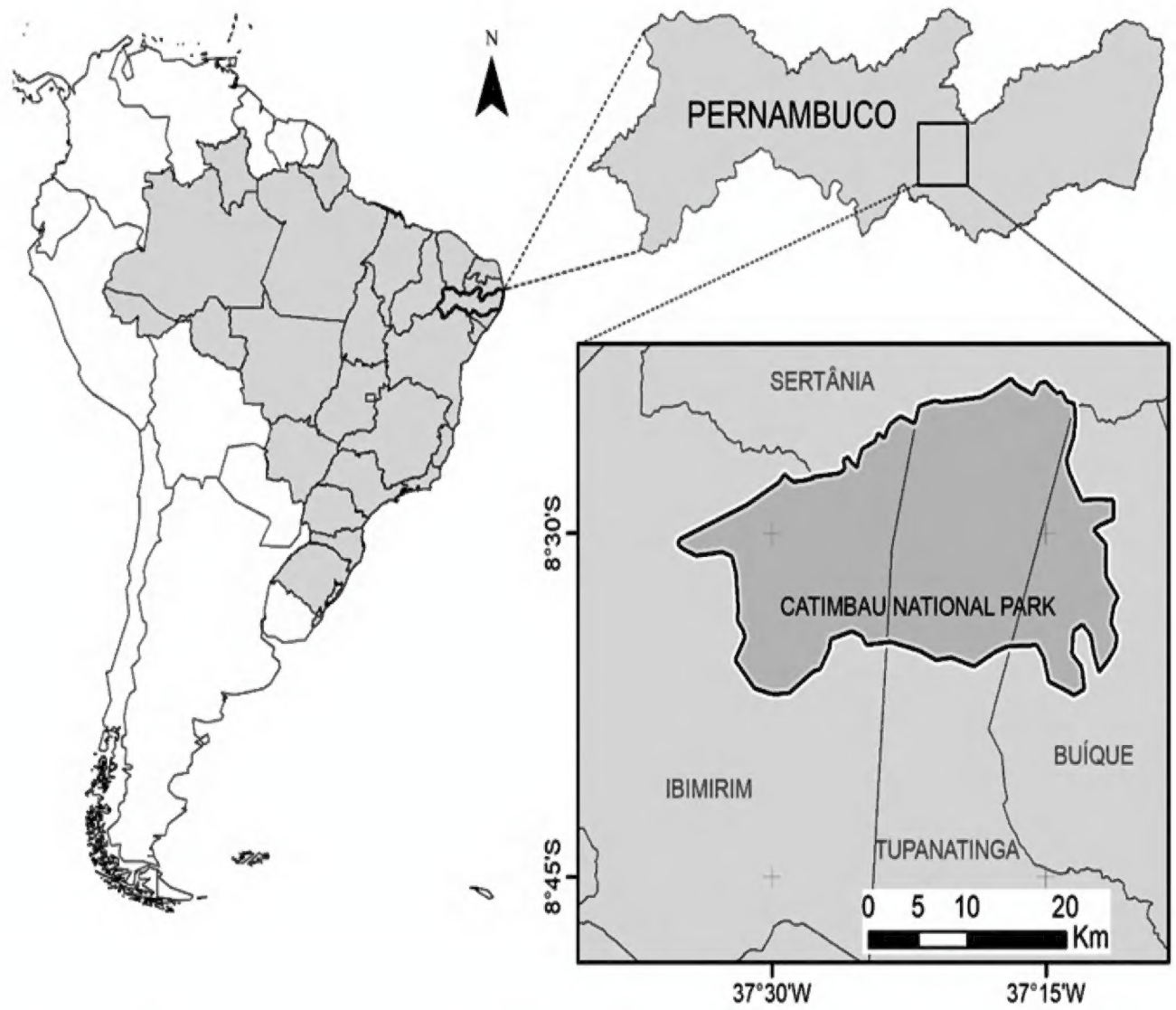

Figure 1. Map of Pernambuco (PE) State in Brazil, location of Catimbau National Park inside the state and the municipalities that border the CU.

Lizards' collection and processing

Individuals were collected by active search along a sandy trail approximately 300 m long. Surveys were conducted at hourly intervals over three days. Active searches were carried out during the day (from 9:00 h to 14:00 h) and at night (from 16:00 h to 20:00 h), with collections and observations made by a pair of observers, conducted monthly from September 2018 to August 2019 to record seasonal variations. We recorded the sex (female or male), and age (adult, juvenile, or sexually immature) of each individual. Sexual maturity was determined according to the gonad volume (< 0.1 mm^3 for ovaries and < 1 mm^3 for testicles) (Kolodiuk et al. 2010; Ragner et al. 2014). After capture, the collected individuals were weighed and subjected to a lethal injection of ketamine (10 mg/kg + 0.1–0.3 mg/kg). Due to the lack of significant variations in climatic conditions (precipitation and temperature) between the years (from 2014 to 2019) (see Suppl. material 1), the present study also incorporates data from individuals that were previously captured in Catimbau National Park in 2014 and curated at the Herpetological Collection of the Federal University of Paraíba, UFPB). The capture and euthanization procedures were standardized for both sampling years.

After euthanization, the following morphometric variables were recorded using a digital caliper (0.01 mm): snout-vent length (SVL), body width (BW; at the broadest point), body height (BH; at the highest point), head height (HH; at the highest point), head width (HW; at the broadest point), head length (HL; from the tip of the snout to the anterior margin of the ear-opening), tail length (TL; from cloaca to the tip of tail), forelimb length (FL; from the forepaw-body bond to the tip of lamella), and hindlimb length (HLL; from the hind leg body bond to the tip of the lamella) (Colli et al. 2003). Tail length was excluded from the analyses because most individuals had broken tails or signs of an earlier autotomy. After morphometric measurements were recorded, we removed the stomach contents of all individuals through a longitudinal incision from the throat to the vent. The contents were analyzed, and the prey was identified at the lower taxonomic level possible (order). In addition, the stomach contents of 48 individuals were refrigerated prior to biochemical analyses and 83 contents were preserved in 70% alcohol.

The stomach contents were subjected to biochemical tests to measure the total protein, lipid, and glycogen proportion (Sönmez and Gülel 2008). The contents were macerated in 0.5 mL of sodium phosphate buffer (pH 7.2; 0.1 mM) and centrifuged at 3,000 × *g* for three minutes. The supernatant (100 µL) was removed from the resulting homogenates for protein measurement and the remaining homogenates were centrifuged again for lipids and glycogens. The Bradford method (Bradford 1976) and bovine serum albumin (BSA) were used as standards, with absorbance measured at 595 nm to determine the total protein quantity. Using the van Handel method (Van Handel 1985 a, b), 200 µL of the homogenates was added to 200 µL of sodium sulfate and 800 µL of methanol and chloroform (1:1) and centrifuged at 3,000 × *g* for three minutes in each experiment. The precipitate was used for glycogen analysis and the supernatant was transferred to a test tube for lipid analysis. Lipids were estimated spectrophotometrically

using the sulfo-phospho-vanillin method (Hiai et al. 1976), while glycogen content was estimated using the anthrone-sulfuric acid method (Hiai et al. 1976), with both absorbances measured at 625 nm. Stomach contents with results outside of their respective confidence intervals for protein (0.095–0.602 µg/mL), lipid (0.039–0.603 µg/mL), and glycogen (0.226–1.575 µg/mL) were excluded from the analysis (Gasco et al. 2016). The results inserted on the confidence intervals were converted to cal/mg, using the dataset established by a calorimeter. Individual collection and all procedures of the present study were authorized by the Animal Use Environmental Agency (SISBIO # 64455-1 and SISBIO # 29550-4) and the Ethics Committee (CEUA UFRPE 123/2018).

Data analysis

The packages *corrplot* and *caret* were used for morphometric analyses and the package *mice* for missing data imputation (Van Buuren and Groothuis-Oudshoorn 2011; Penone et al. 2014). We tested sexual dimorphism for one single analysis of variance (ANOVA), which was tested using an adjusted linear model wrapping the lowest correlated measurements (< 0.7), as well as their interactions for both groups (females and males), whereas the highest correlated measurements (> 0.7) were excluded from the analysis (Chambers et al. 1992). The less correlated measurements were isolated and subjected to nonmetric multidimensional scaling (NMDS), coupled with a PERMANOVA test, using *vegan* and *ggpubr* packages. This analysis was performed to determine distance and group overlap. All morphometric variables were log-transformed (base 10) before analysis to obtain normality.

We recorded the length and width of the prey from the stomach contents using a digital calliper (0.01 mm) so long as it was not too fragmented. These measurements were used to estimate prey volume as an ellipsoid ($V = 4 / 3\pi [w / 2]^2 . [l / 2]$). We calculated the frequency, numeric and volumetric percentages, and relative importance index (RII) for each prey category. Estimates considered individual stomachs (IIS = (%N + %V)/2) and pooled stomachs (IPS = (%N + %V+ %F)/3), where N is the numeric percentage, V is the volume pooled percentage, and F is the occurrence frequency.

Trophic niche diversity was calculated using the standardized Levin's index (Ba). $Ba = (B-1) / (n-1)$, where (n) is the prey category and (B) represents Levin's index of niche breadth: $B = 1 / \Sigma pi^2$, where (p) is the proportion of each prey category (i). Ba ranges from 0 to 1, with values close to '1' indicating a generalized diet and values close to '0' specialized (Mamou et al. 2019). The index was used to verify the overall diet diversity and differences between seasons, with respect to the dry season (Bads) and the rainy season (Bars). We calculated diet overlap between females and males and dry and rainy seasons, which were estimated through the numeric and volumetric niche overlap indices (Pianka 1973) using the following formula in the R package *spaa*: $OFM = OMF = \sum pMipFi/\sqrt{(p2Mi)}\sqrt{(p2Fi)}$, where pMi is the male proportion prey category i, and pFi is the female proportion prey category i.

We used the individual-level diet variation index (E) to analyze the presence and measurement of the degree of individual specialization (IS) (Araújo et al. 2008). This index is based on network theory and quantifies the average density of connections, corresponding to the average dissimilarity among individuals (interindividual variation condition). The values of E ranged from 0 (individuals with identical diets) to 1 (individuals with different diets), sharing dietary components to different degrees. The lower the number of consumed items, the greater the likelihood that individuals will show more varied stomach contents (Carvalho-Rocha et al. 2018).

We tested whether individual specialization was present for its correlation with sex and seasonal variation, considering prey number. Based on the PCA component scores, we calculated a matrix (Suppl. material 2) of pairwise Euclidean morphological distances among all individuals. We also calculated the PS index, where pik and pjk represent the proportions of item category k in the diets of individuals i and j, respectively, to generate a pairwise diet overlap matrix among the individuals. Finally, the correlation between the diet overlap matrix and seasonal distance matrices was tested using a simple Mantel test (10,000 simulations) (Araújo et al. 2007). We would expect a negative correlation between matrices of diet overlap and seasonal distances if functional seasonality affected individual diets, indicating that individuals collected in the same season (small Euclidean distances) also show similar diets (high diet overlap), regardless of sex.

A network analysis was performed to describe the resource patterns used by each individual. First, we built an individual resource matrix (R), with individuals in columns and resource categories in rows. Each element rij of R was filled with the number of ingested prey of resource j by individual i. From R, we depicted bipartite networks comprising two sets of nodes (individuals and resource categories) and lines linking each individual to each of their consumed resources (Pires et al. 2011). Then, we described resource-sharing patterns between individuals testing for nestedness and modularity in the individual-resource networks. Nestedness consists of network propriety, which indicates the presence of highly connected nodes and other less connected nodes that interact in most cases with only at highly connected subset of nodes (Guimarães et al. 2006). Here, nestedness indicates how much of the most specialized diet represents a subset of the more generalized ones (Araújo et al. 2010; Pires et al. 2011). All analyses were performed using *ade4*, *bipartite* and *RInSp* packages.

Variations between sex and season were analyzed considering individual stomach content according to the number and volume of ingested prey (Garda et al. 2014). Generalized linear models (GLM) were produced using the number and volume of ingested prey as predictive models to test the variance between females and males and dry and rainy seasons. The GLM was used to avoid

differences between sampling months and, consequently, captured individuals (predator and prey), using *DHARMa* and *readxl* packages (Zuur et al. 2009). A linear regression test (r^2) was performed using SVL as an independent variable (Vitt 1995; Mesquita et al. 2015) to analyze the correlation between morphology and ingested prey volume.

We also compared the energy content (proteins, lipids, and glycogen) between the sexes and seasons using GLM analysis. Both factors (sex and season) were tested, considering proteins, lipids, and glycogen as variants to verify differences in energy content according to their interactions. The factors were tested simultaneously and separately to verify their influence on the energy content. The relationship between the number and volume of prey and energy values was measured by a multiple regression test (r^2) using protein, lipids, and glycogen as dependent variables to associate the condition of the overall stomach content (Mesquita et al. 2015). Statistical analyses were performed using the R program (v3.6.1 R Development Core Team 2019), and the individual resource networks were built in Pajek (<Networks/Pajek (uni-lj.si)>).

Results

A total of 83 individuals were collected throughout the sampling months, and another 74 were obtained from scientific collections, giving a total sample size of 157 individuals, composed of 63 females (40.1%), 68 males (43.3%), and 26 juveniles (16.5%). The average morphometric measurements for both females and males are shown in Table 1, with the smallest reproductive individuals having 34 mm (SVL). The least correlated measures (HLL, HW, HL, HH, and BH) indicated a lack of significant variations in morphology between sexes (ANOVA $F_{2,129} = 21.86$, P = 0.74). The NMDS analysis pooled adult individuals (females and males) into similar groups, revealing high overlap for all measures analyzed, presenting low variation between mature individuals (Fig. 2), indication lack of sexual shape dimorphism (MANOVA $F_{2,129} = 1.23$, P = 0.26).

Table 1. Average morphometric measurements for males and females *Gymnodactylus geckoides*, sampled between September 2018 and August 2019 and 2014, in Catimbau National Park (PE). Values represent mean ± standard deviation, and range of variables of each body shape measured (mm).

Variables	Females (n = 63)	Males (n = 68)
Snout-vent length	40.03 ± 4.92 (30.95 – 47.25)	40.93 ± 2.74 (32.11 – 45.74)
Body width	8.35 ± 1.67 (5.74 – 13.3)	8.02 ± 1.01 (5.84 – 9.79)
Body height	5.71 ± 1.26 (4.06 – 8.71)	5.64 ± 0.99 (4.04 – 7.74)
Head height	4.31 ± 0.59 (3.33 – 5.44)	4.50 ± 0.75 (3.42 – 6.69)
Head width	6.18 ± 0.77 (5.02 – 8.98)	7.13 ± 0.89 (5.15 – 8.52)
Head length	10.73 ± 1.50 (8.64 – 14.44)	10.36 ± 1.59 (8.81 – 13.66)
Forelimb length	11.15 ± 2.18 (8.20 – 15.58)	11.56 ± 2.14 (8.18 – 15.94)
Hindlimb length	14.75 ± 2.42 (11.07 – 19.06)	15.12 ± 2.10 (11.24 – 18.84)

The diet dataset was obtained from dissected stomachs of 131 individuals: 56 females (42.7%), 66 males (50.3%), and nine juveniles (6.9%). Ten individuals (7.63%) had an empty stomach. Data on 1,035 food items were compiled and classified into 18 different categories, averaging 7.90 items/stomach. The diet was mainly composed of invertebrates (insects and arachnids) with occasional mineral, sand, and vegetal sediments (Table 2). The most abundant item was Isoptera, which represented over two-thirds of the prey, almost one-third of the prey frequency, and half of the prey volume. Coleoptera, Blattodea, and Orthoptera were among the four most important categories, considering the pooled and individual stomach contents.

Considering the pooled stomachs described above, Isoptera and Coleoptera were the most significant numerically and volumetrically. Both indices (iis and ips) revealed that half of the *G. geckoides*s diet comprised only Isoptera. In addition, Levi's index indicated low trophic niche breadth (Ba = 0.27). Regarding seasonality, niche breadth revealed lower diversity of prey type ingested during the dry season (Bads = 0.52) than during the rainy season (Bars = 0.68). Diet quantity showed a high volume (0.78) and frequency (0.96) overlap between sexes, indicating that similar items were consumed by females and males, despite the niche breadth difference between seasons.

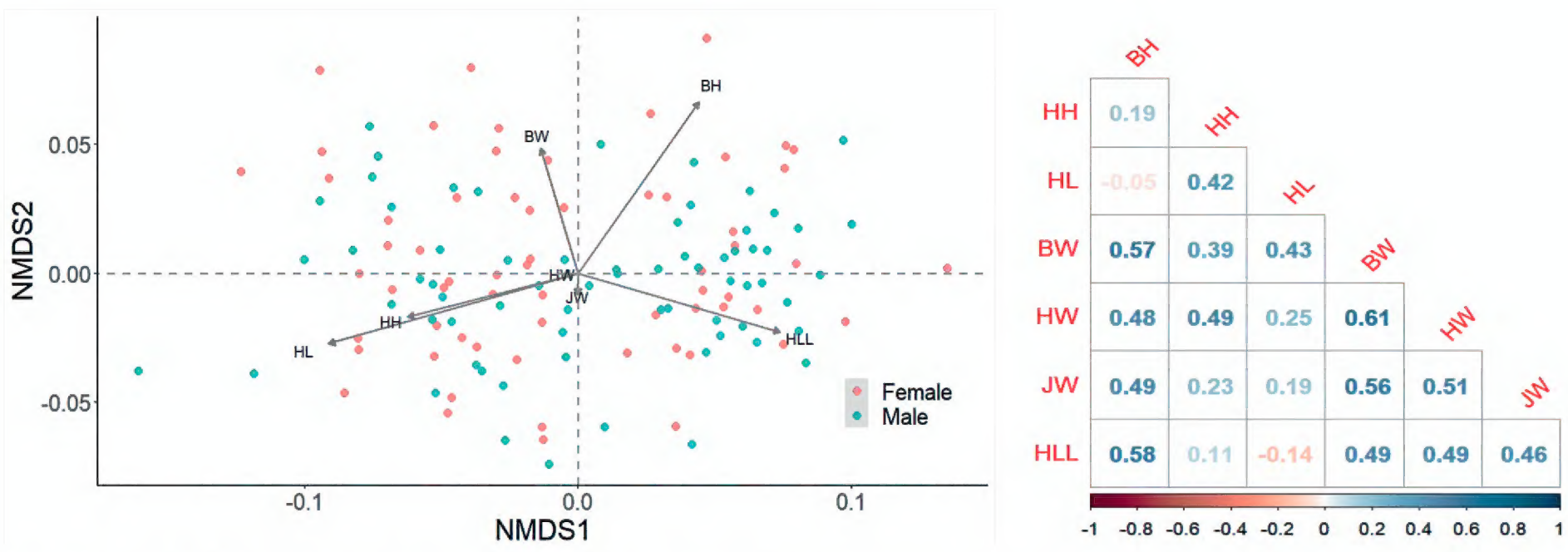

Figure 2. NDMS Analysis for females and males of *Gymnodactylus geckoides* in Catimbau National Park (PE), using log – transformed of HLL, HW, HL, HH, BH and Jaw Width (JW) sizes. Correlation analyzes revealed negative correlation, between HLL and HL, and HL and BH (-0.05 and -0.14, respectively), while other measurements revealed positive correlation (from 0.11 to 0.61).

Table 2. Diet composition of the 131 *Gymnodactylus geckoides* captured in Catimbau National Park (PE). n = prey number; v = prey volume; SD = Standard deviation; f = number of stomachs which contained the prey; ips – Importance index of pooled stomachs; iis – Importance index of individual stomachs.

Category	Pooled stomachs							Individual stomachs				
	F	f%	N	n%	v	v%	ips	n±SD	n%±SD	v±SD	v%±SD	iis
Arachnid												
Aranae	28	11.72	36	3.48	237.55	2.77	5.99	0.27 ± 0.53	3.48 ± 0.05	1.81 ± 16.7	2.77 ± 0.19	3.13
Pseudoscorpion	3	1.26	3	0.29	3.02	0.04	0.53	0.02 ± 0.00	0.29 ± 0.00	0.02 ± 1.36	0.04 ± 0.02	0.17
Insect												
Blattodea	10	4.18	11	1.06	1390.76	16.20	7.15	0.08 ± 0.32	1.06 ± 0.03	10.62 ± 323.64	16.20 ± 3.77	8.63
Coleoptera	58	24.27	82	7.83	212.88	2.48	11.53	0.63 ± 0.75	7.92 ± 0.07	1.63 ± 8.28	2.48 ± 0.10	5.20
Diptera	5	2.09	6	0.58	4.62	0.05	0.91	0.05 ± 0.45	0.58 ± 0.04	0.04 ± 0.00	0.05 ± 0.00	0.32
Hemiptera	2	0.84	5	0.48	58.30	0.68	0.67	0.04 ± 0.71	0.48 ± 0.07	0.45 ± 39.13	0.68 ± 0.46	0.58
Hymnoptera	25	10.46	45	4.35	313.58	3.65	6.15	0.34 ± 1.08	4.35 ± 0.10	2.39 ± 51.55	3.65 ± 0.62	4.00
Isoptera	66	27.62	802	77.49	4239.49	49.37	51.49	6.12 ± 12.12	77.50 ± 1.16	32.36 ± 146.13	49.37 ± 1.70	63.44
Lepdoptera	5	2.09	5	0.48	39.28	0.46	1.01	0.04 ± 0.35	0.48 ± 0.03	0.30 ± 215.99	0.46 ± 2.52	0.47
Mantodea	1	0.42	1	0.10	–	–	–	0.01 ± 0.00	0.10 ± 0.00	–	–	–
Neuroptera	1	0.42	1	0.10	107.63	1.25	0.59	0.01 ± 0.00	0.10 ± 0.00	0.82 ± 0.00	1.25 ± 0.00	0.68
Odonata	5	2.09	6	0.58	230.57	2.68	1.79	0.05 ± 0.55	0.58 ± 0.05	1.76 ± 42.69	2.69 ± 0.50	1.64
Orthopthera	15	6.28	16	1.55	1052.57	12.26	6.69	0.12 ± 0.26	1.55 ± 0.02	8.03 ± 121.17	12.26 ± 1.41	6.91
Larvae												
Coleoptera	2	0.84	3	0.29	98.94	1.15	0.76	0.02 ± 0.71	0.29 ± 41.92	0.76 ± 0.07	1.15 ± 0.49	0.72
Insect larvae	6	2.51	6	0.58	129.71	1.51	1.53	0.05 ± 0.00	0.58 ± 0.00	0.99 ± 39.37	1.51 ± 0.46	1.05
Lepdoptera	5	2.09	5	0.48	463.86	5.40	2.66	0.04 ± 0.00	0.48 ± 0.00	3.54 ± 87.88	5.4 ± 1.02	2.94
Odonata	1	0.42	1	0.10	4.82	0.06	0.19	0.01 ± 0.00	0.10 ± 0.00	0.04 ± 0.00	0.06 ± 0.00	0.08
Vertebrate												
Squamata	1	0.42	1	0.10				0.01 ± 0.00	0.10 ± 0.00			
Total	1035											

Figure 3. Qualitative individual-resource matrices and networks of *Gymnodactylus geckoides*, at Catimbau National Park. In the matrices, cells indicate a given individual in their respective groups, regarding sex (female and male) and seasonality (dry and rainy) (rows) consuming distinct prey types in different intensity (columns). In the networks, ellipses represent individuals, triangles represent resources and lines represent the consumption of a given resource by an individual according to seasonality.

We found low individual-level diet variation index values, indicating a similar diet between females and males, with lower variations during the dry season ($E = 0.18$) than during the rainy season ($E = 0.27$). This index, as well as the network analysis, indicated variation in individual specialization according to seasonality, with females and males displaying a high frequency of Isoptera ingestion during the dry season, and other prey types (Coleoptera, Araneae, Hymenoptera, and Orthoptera) being consumed at higher frequencies during the rainy season (Fig. 3).

Regarding individual stomachs, the GLM did not reveal significant variations between sexes, for both prey number (β ± SE = -0.038 ± 0.025, z = -1.509, p = 0.849; females: 0.90 ± 1.11, males:0.70 ± 0.97) and volume

(β ± SE = 0.147 ± 0.378, z = 0.389, p = 0.697; females: 1.78 ± 2.21, males:1.39 ± 2.17). Regarding seasonality, the GLM revealed significant variations in prey number (β ± SE = -0.150 ± 0.047, z = -3.205, p < 0.001; dry season:1.29 ± 1.14, rainy season:0.79 ± 0.69) and volume (β ± SE = 0.005 ± 0.002, z = 1.833, p = 0.05; dry season:0.76 ± 0.41, rainy season:1.02 ± 0.57). Therefore, both females and males had similar diet proportion, with a greater quantity of prey consumed during the dry season and a higher volume consumed during the rainy season. Consistent with previous studies, the capacity for consumption of higher prey volumes increased with predator morphology. However, linear regression revealed a weak relationship between SVL (R^2 = 0.03, $F_{1,113}$ = 4.33, P = 0.03) and HW (R^2 = 0.05, $F_{1,113}$ = 6.42, P < 0.01), indicating a random pattern of prey ingestion by *G. geckoides*.

Forty-eight individuals were evaluated for the biochemical tests, with 24 analyzed for the dry season (14 females and ten males) and 24 for the rainy season (13 females and 11 males). Regardless of season and sex, the average protein was 0.15 ± 0.07 cal/mg (n = 37; range = 0.04–0.32); lipids 1.92 ± 1.59 cal/mg (n = 32; range = 0.36–6.19), and glycogen 3.54 ± 1.95 cal/mg (n = 35; range = 1.09–7.61). The GLM test did not reveal significant variation in the amounts of protein and lipid between sexes and seasons, indicating similar rates of consumption between females and males and between dry and rainy seasons (Table 3 and Fig. 4). A slightly higher rate was recorded for proteins in females during the rainy season, whereas males displayed higher rates during the dry season. Regarding lipids, a slightly higher rate was recorded in females in both seasons, with higher values obtained in the dry season. In contrast, glycogen exhibited significant variance according to season, with greater amounts during the rainy season for both sexes (Table 3 and Fig. 4).

Table 3. GLM tests for energetical support of Proteins, Lipids and Glycogen in stomach content of *G. geckoides*, regarding gender (Female and Male) and season (Dry and Rainy) in Catimbau National Park (PE). Tests performed with each factor analyzed (Sex and Season), once tested together for each component analyzed. * Indicates significant variation (< 0.05).

Biochemical	Sex (Female and Male)			Season (Dry and Rainy)		
	Estimate ± SE	z- value	p-value	Estimate ± SE	z- value	p-value
Intercept	0.119 ± 0.952	0.126	0.900	-1.206 ± 0.996	-1.210	0.226
Protein	2.003 ± 4.284	0.468	0.640	-0.334 ± 4.486	-0.075	0.940
Lipid	-0.166 ± 0.210	-0.790	0.430	-0.745 ± 0.218	-0.341	0.733
Glycogen	-0.111 ± 0.157	-0.711	0.477	0.416 ± 0.171	2.420	< 0.01*

Multiple regression tests showed positive results and a weak correlation between nutritional substances and stomach content. Proteins exhibited the highest correlation (45%; CI = 30.67; R^2 = 0.45), followed by glycogen (10%; CI = 5.23; R^2 = 0.10), and lipids (8%; CI = 0.67; R^2 = 0.08), with no significant correlation (p > 0.05). Regarding prey type, we investigated reference values

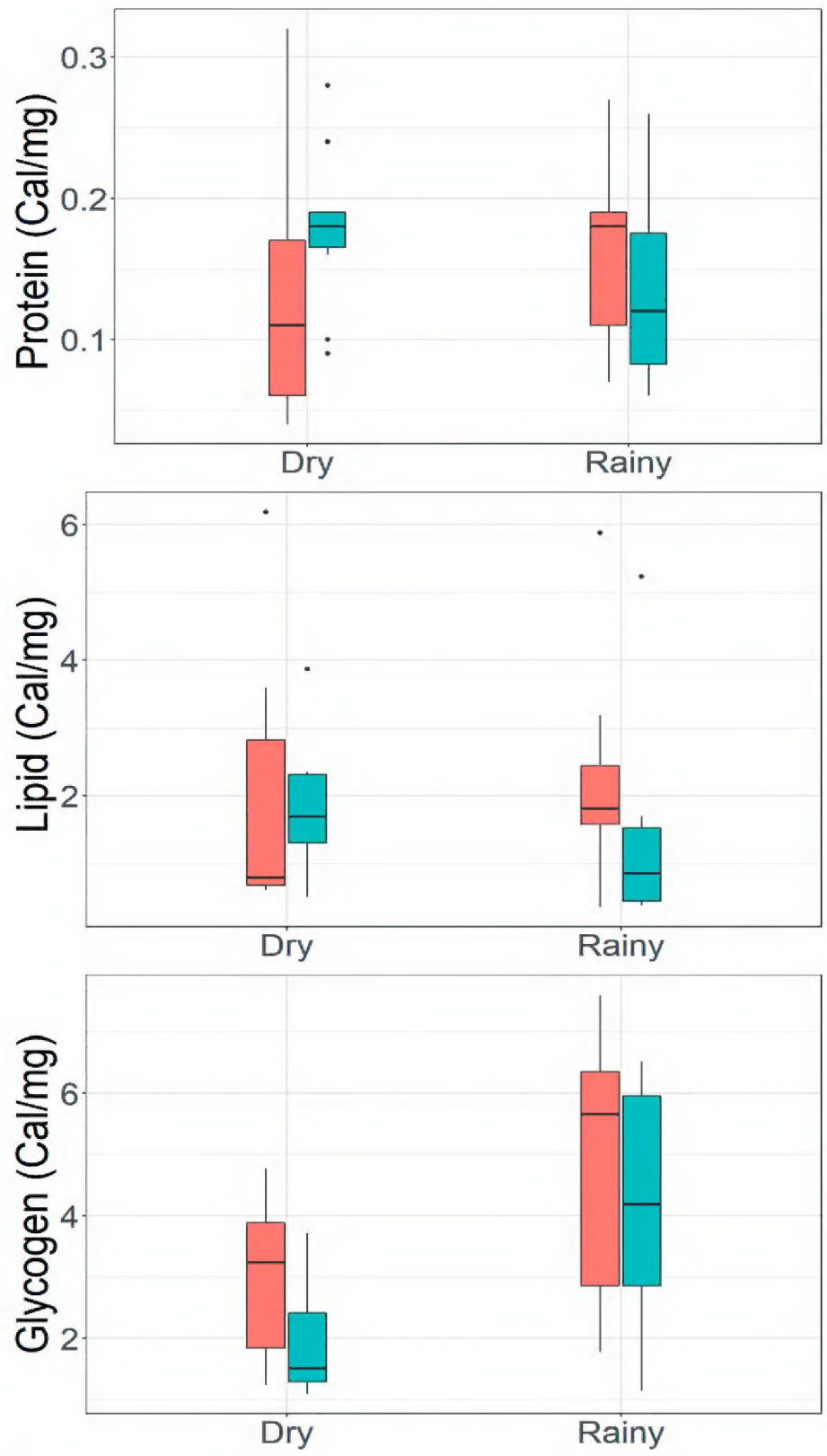

Figure 4. Variation of Proteins, Lipids and Glycogen regarding females (red boxes) and males (blue boxes) and seasons (dry and rainy), in stomach content of *G. geckoides* sampled, in Catimbau National Park (PE).

for four different morphotypes (Isoptera, Orthoptera, Coleoptera, and Lepidoptera larvae), which were found individually in the stomach contents. Despite presenting high importance index, Isoptera yielded three–five times less energy in protein content, three–ten times less energy in lipids, and three–five times less energy in glycogen than other prey types consumed at a lower frequency (Table 4).

Table 4. Reference values of energetical support, for protein, lipid and glycogen, of different prey types found isolated in individuals stomachs of *Gymnodactylus geckoides* sampled in Catimbau National Park (PE).

Morphotype prey	Protein (cal/mg)	Lipid (cal/mg)	Glycogen (cal/mg)
Isoptera	0.03	0.31	0.33
Orthoptera	0.12	3.43	1.31
Coleoptera (larvae)	0.09	1.14	0.81
Lepidoptera (larvae)	0.16	1.08	1.81

Discussion

Sexual dimorphism was absent in our study. In lizards, sexual dimorphism may be related to different microhabitats, diets, and reproduction (sexual selection and clutch size) (Huey and Pianka 1981; Vitt 1986; Mesquita et al. 2015). However, since females and males displayed similarities in the resources used (microhabitat and feeding), considering the gregarious distribution recorded during fieldwork and fixed clutch size in females (one egg), it is not surprising that *G. geckoides* lack sexual dimorphism. In addition, the lack of morphological variation between females and males indicates that both sexes are subjected to similar environmental adaptive pressures (Serrano-Cardozo et al. 2007). Individuals in the study population reached sexual maturity above 34 mm (SVL).

A similar diet was recorded between females and males of *G. geckoides*, with the same quantities of prey ingested. Half of the diet is comprised of a single prey type (Isoptera). Isoptera constitute a prominent insect order, mainly in semiarid biomes such as Caatinga (Vitt 1995; Vasconcellos et al. 2010a), displaying a high nest frequency (90 nests per hectare – Caatinga) (Vasconcellos et al. 2010a; Souza-Oliveira et al. 2017). Because Isoptera are usually found in microhabitats with a high concentration of organic material, such as leaf litter, shrubs, and fallen trunks (Colli et al. 2003; Vasconcellos et al. 2010a), which constitutes microhabitats likely occupied by both females and males of *G. geckoides* (Vitt 1995), it is not surprising that a large frequency of Isoptera is included in their diet. In addition, the importance of this prey type and their constant frequency during the year, considering that geckos are highly chemosensory (Schewnk 1993; Colli et al. 2003), indicate that Isoptera display a guaranteed feeding source for both females and males of *G. geckoides*, resulting in a high food niche overlap between females and males.

This lizard consumed both sedentary and active prey. Generally, generalist lizards adopt a mixed foraging strategy (ambush and active forager) (Cooper 1995; Vitt 1995), modifying their hunting strategies according to the pressures imposed by the environment (Huey and Pianka 1981; Ferreira et al. 2017), passing away with lizard specimens specializing in certain food items, or displaying a particular foraging mode (Pough et al. 1998). Therefore, the present study indicates that variations in *G. geckoides* behavior could be associated with climate and landscape conformational changes in the Caatinga biome, with changes proportional to different prey types and other factors, such as their abundance (Huey and Pianka 1981; Díaz and Carrascal 1993; Ferreira et al. 2017).

The seasonal variation of the diet involved prey type, as well as the numbers and volume ingested. Our results showed individual-level diet variation patterns in *G. geckoides*, implying more similar diets among individuals during the dry season than during the rainy season (Bolnick et al. 2002; Bolnick et al. 2003; Martins et al. 2008). Therefore, *G. geckoides* tend to be more proactive during the dry season, seeking and establishing territory close to Isoptera nests. On the other hand, as long as food availability increases with rainfall levels, *G. geckoides* seem to display fairly static stationary behavior, often with a range of prey types, as well as prey number (Díaz and Carrascal 1993; Martins et al. 2008; Ferreira et al. 2017). These variations in feeding habits seem to help *G. geckoides* remain adaptable to environmental seasonality, mainly considering prey availability (Desfilis and Font 2002; Vasconcelos et al. 2010a, b; Ferreira et al. 2013), which is also suggested by the variations in niche breadth between seasons (Toft 1985; Ferreira et al. 2017).

Biochemical tests enabled the description of the average available protein, lipid, and glycogen, establishing primary nutritional values from some prey types individually. Our records of isolated prey indicated that one or two units of prey such as Orthoptera and Lepidoptera larvae may yield the same calories as 5 to 11 units of other prey types such as Isoptera, reinforcing theories that there could be variations of energy levels provided by different prey types ingested, as well as a particular fondness for energetically advantageous prey, mainly regarding an energy-expensive life stage (Costa et al. 2008; Souza-Oliveira et al. 2017). On a progressive scale, glycogen is first metabolized into glucose. In the absence of circulating glucose, lipids are released for energetic metabolism, generating an eco-biochemical cause-and-effect cycle (hypercaloric prey selection generating energetic absorption, leading to more efficient and greater lizard fitness) (Pafilis et al. 2007). Therefore, the ingestion of energetically advantageous prey seems to make available more energy with a lower number of prey ingested (Pafilis and Valakos 2004; Pafilis et al. 2007).

Our results indicated that protein and lipid levels did not vary significantly with seasonality. In Lepidosauria, some species seem to display digestion processes that are highly dependent on body temperature (Harwood 1979; Pafilis and Valakos 2004), whereas other species' digestion processes may be insensitive to body temperature (Zimmerman and Tracy 1989; Bedford and Cristian 2000). Sugars constitute the most important energy component in the diet of lizards, presenting the most direct energy source (Chapman 1998; Pafilis and Valakos 2004). According to Scocyzylas (1978) and Berne and Levy (1996), the higher activity of sugar-digesting enzymes in warmer environments could be explained by the fact that optimum temperature for amylase in Lepidosauria is over 40 °C. However, since the environmental temperature does not display significant variation in Caatinga despite high seasonality, sugar digestion probably does not seem to be affected by body temperature in *G. geckoides*, maintaining those temperatures at similar levels in both dry and rainy seasons (Comm. Pess. Leonardo P.C. Oitaven). Lipids are stable organic compounds, only slightly soluble in water and require complex and time-consuming, emulsification and catabolic procedures (Pafilis and Valakos 2004). According to Stryer (1998), many intestinal enzymes, as well as lipolytic enzymes, tend to reach maximum activity at 42 °C, and are much more effective at higher temperatures. Bonded to the low variation in

body temperature, lipids seem to be consumed at similar rates in both seasons by *G. geckoides*, possibly used at a lower frequency compared to glycogen, which could also be applied to protein absorption (Pafilis and Valakos 2004; Pafilis et al. 2007). Therefore, the lower glycogen levels recorded during the dry season are probably more associated with higher energy demand for the lizards due to feeding search (Pafilis et al. 2007).

Individuals tend to spend little energy capturing prey and are more selective according to the increase in prey availability (Díaz and Carrascal 1993). For *G. geckoides*, the energy difference seems to be offset by both prey number and volume ingested, with individuals able to invest in greater numbers of smaller preys, ingested at higher frequency, as well as a smaller number of bigger preys, consumed at lower frequency (Vitt et al. 2001; Mamou et al. 2019). Therefore, the present study indicates plasticity in *G. geckoides'* behavior, with individuals alternating their hunting strategies, strongly bonded to environmental restrictions (Cooper 1994; Ferreira et al. 2017).

Taken together, the present study represents an effort to understand the trophic ecology, such as energy values, from a new perspective, presenting the prey content of *G. geckoides*. The present study also reinforces the importance of further studies using lizards and other vertebrates as models to understand their feeding strategies, as well as plasticity in seasonal environments. The lack of this information for Brazilian species hinders the development of functional management plans for biodiversity conservation.

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Supplementary material 1

Table S1

Authors: Leonardo Oitaven, Sydnei Calado, Hilton da Costa, Glaucilane Cruz, Juan S. Monrós, Daniel Mesquita, Álvaro A. Teixeira, Valéria Teixeira, Geraldo J. de Moura

Data type: Excel file

Explanation note: Climatological variations in Catimbau National Park.

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Link: https://doi.org/10.3897/herpetozoa.35.e87199.suppl1

Supplementary material 2

Matrix

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Data type: Text file (.txt)

Explanation note: Matrix for dataset comparison.

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